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Population Modelling of Black Redhorse (*Moxostoma duquesni*) in Canada

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Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) had assessed Black Redhorse (*Moxostoma duquesnei*) as Threatened in Canada (COSEWIC 2005). Here we present population modelling in support of the upcoming reassessment of the species, and incorporate new Canadian data collected since the previous assessment in 2005. Results include a sensitivity analysis and determination of recovery targets for population abundance and required habitat. Our analyses demonstrated that the dynamics of Canadian Black Redhorse populations are particularly sensitive to perturbations that affect survival of immature individuals (from hatch to age 4), and early adults (ages 2-8). Harm to these portions of the life cycle should be minimized to avoid jeopardizing the survival and future recovery of Canadian populations. Based on an objective of demographic sustainability (i.e., a self-sustaining population over the long term), we propose a population abundance recovery target of at least 1700 adult Black Redhorse (ages 4+), and 3900 juveniles, requiring 14.5 ha of suitable habitat. Targets for alternative risk scenarios ranged from ~800 adults and 6.5 ha to 5800 adults and 49 ha.

Modélisation des populations de chevalier noir (*Moxostoma duquesni*) au Canada

RÉSUMÉ

Le Comité sur la situation des espèces en péril au Canada (COSEPAC) a déterminé que le chevalier noir (*Moxostoma duquesnei*) est une espèce menacée au Canada (COSEPAC 2005). Le présent document fournit la modélisation de la population à l'appui de la réévaluation à venir de l'espèce et incorpore les nouvelles données canadiennes recueillies depuis la dernière évaluation en 2005. Les résultats comprennent une analyse de sensibilité et une détermination des cibles de rétablissement pour l'abondance de la population et l'habitat requis. Nos analyses prouvent que la dynamique des populations de chevaliers noirs est particulièrement sensible aux perturbations qui affectent la survie des individus immatures (de l'éclosion à l'âge 4) et des jeunes adultes (âges 2 à 8). Il faut réduire le plus possible les dommages à ces stades du cycle de vie afin d'éviter de mettre en péril la survie et le rétablissement futur des populations au Canada. En nous basant sur un objectif de durabilité démographique (c.-à-d. une population autonome à long terme), nous proposons une cible de rétablissement de l'abondance d'au moins 1 700 chevaliers noirs adultes (âges 4+) et de 3 900 juvéniles, ce qui nécessite 14,5 ha d'habitat convenable. Les cibles des autres scénarios de risques varient de 800 adultes et 6,5 ha à 5 800 adultes et 49 ha.

INTRODUCTION

Black Redhorse (*Moxostoma duquesnei*) was first designated as *Threatened* by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 1988. This status was re-examined and confirmed in May 2005 (COSEWIC 2005). In 2007 DFO conducted a Recovery Potential Assessment (RPA; DFO 2007) to assess the species; it was not listed by DFO at this time.

DFO has developed a pre-COSEWIC process to compile and present new information in support of COSEWIC status reports. In advance of the 2013 COSEWIC reassessment of the status of Black Redhorse, we present population modelling of the species that updates the modelling conducted in support of the 2007 RPA (Vélez-Espino and Koops 2008; Vélez-Espino and Koops 2009a) using new sampling data collected since the 2007 RPA. Specifically, we assess the sensitivity of Black Redhorse population growth to perturbations in survival and fecundity of different life stages, and determine the minimum viable population (MVP) and minimum area required for population viability (MAPV) for the species.

METHODS

Our analysis consisted of three parts: (i) information on vital rates was compiled and used to build projection matrices, using uncertainty in life history to represent variation in the life cycle for stochastic simulations; (ii) we used these matrices in a stochastic perturbation to determine the sensitivity of the population growth rate to changes in each vital rate following Vélez-Espino and Koops (2009a); (Vélez-Espino and Koops 2009b) and (iii) the projection matrices were used to simulate risk of extinction, and to estimate the minimum viable population (MVP) and the minimum area for population viability (MAPV) (i.e., the amount of suitable habitat required to support the MVP).

SOURCES

This work expands on modelling conducted by Vélez-Espino and Koops (2008; 2009a). New data have been incorporated, including aged samples of Black Redhorse from Reid (2009), captured in the Grand River, Ontario. Methodology for the determination of MVP follows Young and Koops (2011), and is compared to that used by Vélez-Espino and Koops (2008).

THE MODEL

Using a matrix approach, the life cycle of Black Redhorse was represented with annual projection intervals and by a post-breeding age-structured projection matrix (Caswell 2001) (Figure 1). New data allowed for age-specific estimation of vital rates, in contrast to Vélez-Espino and Koops (2008), in which information was collapsed into 4 life stages. Elements of the age-structured matrix include the fecundity coefficient of age class j (F_j), and the age-specific annual probability of surviving from age j-1 to age j (σ_j).

Fecundity coefficients (F_j) represent the contribution of an adult in age class j to the next census of age-0 individuals. Since a post-breeding model is assumed, the coefficient F_j includes the annual survival probability of adults from age j-1 to age j (σ_j), as well as the age-specific annual number of female offspring for an individual on their j^{th} birthday (f_j) such that

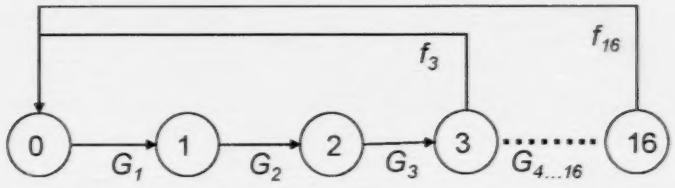
$$(1)\quad F_j = \sigma_j f_j,$$

where f_j is the product of the average fertility (total annual egg count) for a female of age j (n_j), the proportion of females in the population (φ, assumed to be 50% for Black Redhorse), the

proportion of fish that reproduce at age *j* (ρ_j), and the inverse of the average spawning periodicity (T, assumed to be 1 for Black Redhorse):

$$f_j = \eta_j \varphi \rho_j \frac{1}{\mathrm{T}}. \quad (2)$$

a)



b)

$$M = \begin{pmatrix} 0 & 0 & F_3 & \ldots\ldots & F_{16} & 0 \\ G_1 & 0 & 0 & \ldots. & 0 & 0 \\ 0 & G_2 & 0 & & 0 & 0 \\ .0 & 0 & G_3 & \ldots. & 0 & 0 \\ \ldots. & & \ldots. & \ldots & \ldots. & \ldots. \\ 0 & 0 & 0 & \ldots. & G_{16} & 0 \end{pmatrix}$$

Figure 1. Generalized life cycle (a), corresponding age-structured projection matrix (b) used to model the population dynamics of Black Redhorse. Fi represents annual effective fecundities, and σi the survival probabilities from age j-1 to age j.

Parameter estimates

Black Redhorse in the Grand River, Ontario were found to mature as early as 3 years with the majority likely mature by age 4 (Reid 2006). As in Velez-Espino and Koops (2009a), a cumulative binomial distribution was used to estimate the probability of a female maturing at age *j* such that the probabilities of maturing for ages 3, 4, and 5 females were 0.25, 0.75, and 1, respectively. The observed maximum lifespan of Black Redhorse in the Grand River was 16 years (Reid 2009).

Estimates of growth and survival for Black Redhorse in Ontario were based on a von Bertalanffy growth curve fitted to age-at-length data from Reid (2009) (Figure 2). The growth curve relates size and age using the formula: $L_t = L_\infty\ (1 - e^{-k(t-t_0)})$, where L_t is total length at time t, t_0 is the hypothetical age at which the fish would have had length 0, L_∞ is the asymptotic size, and k is a growth parameter. Hatch length was overestimated by the fitted curve to be 40 mm, much larger than the observed mean length of emergence of 8.8 mm (COSEWIC 2005). Therefore, the curve was forced to pass through 8.8 mm at age 0 to allow a more meaningful representation of first year growth (Figure 2). Size-at-age predicted by this curve (Table 1) was used for all subsequent short-lived model calculations. Uncertainty in mean size-at-age was incorporated by calculating bootstrapped confidence intervals on the fitted growth curve (Baty and Delignette-Muller 2009).

Age-dependent mortality was estimated by combining a size-dependent mortality model (Lorenzen 2000) with von Bertalanffy growth parameters and a catch curve analysis of age-frequency data (Hilborn and Walters 1992). Mortality was assumed to decline proportionally with increases in size (Lorenzen 2000) such that

(3) $$M_t = \frac{m_0}{L_t},$$

where M_t and L_t are the instantaneous mortality and mean length at time t, and m_0 is the mortality at unit size (i.e., at $L_t = 1$). If L_t is described by the von Bertalanffy growth curve equation, survival from age j to age j+1 can be calculated by integrating equation (3) and evaluating between j and j+1:

(4) $$s_{j \to j+1} = \left[\frac{L_j e^{-k}}{L_{j+1}} \right]^{m_0 / kL_\infty}.$$

k and L_∞ are parameters of the von Bertalanffy growth equation as evaluated above. The parameter m_0 can be estimated by performing a modified catch curve analysis where logged frequencies are binned based on equation (4), so that m_0 can be described by the slope of the catch curve regression (β), scaled by the von Bertalanffy parameters (equation (6)).

(5) $$\ln L_t + kt$$

(6) $$m_0 = -kL_\infty \beta$$

Weighted catch curve regressions were performed to decrease the bias from rarer, older fish (Freund and Littell 1991; Maceina and Bettoli 1998). Survival from stage j to stage j+1 was calculated using equation (4). Variance for each survival rate was approximated by first translating the standard error of β from the catch curve regression into a standard error for m_0, then applying the delta method (Oehlert 1992) to equation (4) to estimate the variance of the transformed parameter. Survival and fecundity rates for stochastic simulations were drawn from lognormal distributions with mean and variances as described above. Generation time was calculated from the age-specific survival and fecundity estimates as per Caswell (2001), and yielded a generation time of 8.2 years.

The population growth rate resulting from this method of survival estimation was $\lambda = 2.2$. This value is likely larger than the maximum possible growth rate for a species of this size (approximately 1.6) (Vélez-Espino and Koops 2009a). Likely, first year survival is overestimated. We therefore adjusted first year survival to achieve a desired population growth rate. For population sensitivity analysis (see below) we compared results for a maximum population growth rate ($\lambda = 1.6$), a stable population ($\lambda = 1$) and a population declining at the *Threatened* designation rate (see Vélez-Espino and Koops 2009a) of $\lambda = 0.97$.

Fecundity was estimated using the size-at-age, as above, and the equation relating standard length (SL) to fertility (Kott and Rathmann 1985), as used in Velez-Espino and Koops (2009a), where total length (TL) is TL=1.19SL (Reid 2009):

(7) $$\eta = (2.46 \cdot 10^{-6}) SL^{3.713}.$$

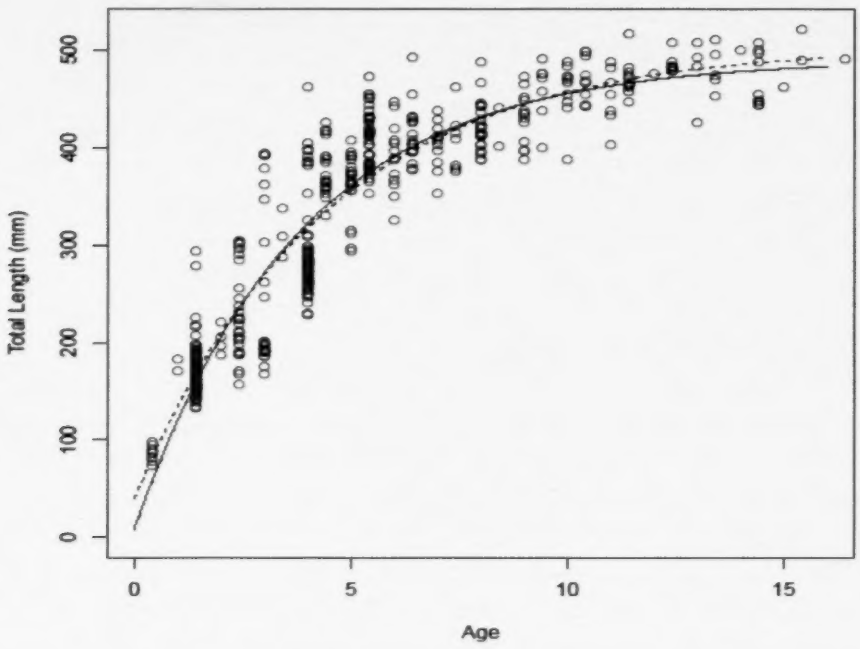


Figure 2. Size-at-age of Black Redhorse sampled from the Grand River, Ontario (Reid 2009) with fitted von Bertallanfy Growth curves either forced (solid) or not forced (dashed) to pass through a hatch size of 8.8 mm.

Table 1. Mean and standard deviation (SD) of total length (TL), fecundity, and survival probability by age for population modelling of Black Redhorse.

Age	TL		Survival		Fecundity	
	mean	SD	mean	SD	mean	SD
0	8.8	NA	NA	NA	NA	NA
1	120.1	1.7	0.00044	0.033	NA	NA
2	205.7	2.5	0.487	0.059	NA	NA
3	271.5	2.6	0.615	0.050	1403	62
4	322.1	2.5	0.677	0.045	2645	89
5	361.0	2.3	0.713	0.041	4039	105
6	390.9	2.2	0.735	0.038	5428	120
7	413.9	2.3	0.750	0.036	6711	150
8	431.5	2.6	0.760	0.035	7838	197
9	445.6	2.9	0.768	0.034	8794	256
10	455.6	3.3	0.773	0.034	9585	318
11	463.6	3.7	0.777	0.033	10228	379
12	469.8	4.0	0.780	0.033	10743	434
13	474.5	4.3	0.782	0.032	11152	484
14	478.2	4.6	0.784	0.032	11473	527
15	481.0	4.8	0.785	0.032	11725	564
16	483.1	5.0	0.786	0.032	11992	595

POPULATION SENSITIVITY

We are interested in the sensitivity of the estimated annual population growth rate (λ) to perturbations in vital rate *v*. Annual population growth rate can be estimated as the largest eigenvalue of the projection matrix (Caswell 2001). Model sensitivity is quantified by elasticities, which are a measure of the sensitivity of population growth rate to perturbations in vital rate *v*, and are given by the scaled partial derivatives of λ with respect to the vital rate:

$$(8) \qquad \varepsilon_v = \frac{v}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial v}.$$

Here, a_{ij} are the matrix elements.

In addition to calculating the elasticities of vital rates deterministically, as described above, we also incorporated variation in vital rates to determine effects on population responses from demographic perturbations. We used computer simulations to (i) generate 5,000 matrices, with vital rates drawn from distributions with means and variances as described above (Table 1) (ii) calculate λ for each matrix; (iii) calculate the ε_v of σ_j and f_j for each matrix; and (iv) estimate mean stochastic elasticities and their parametric, bootstrapped 95% confidence intervals. The elasticity estimation was repeated for growing, stable, or declining populations. The representation of variation and uncertainty differs from Velez-Espino and Koops (2009a), where uncertainty in age at maturity and lifespan were simulated, but variance in survival and fecundity was not. Here, lifespan is fixed, and uncertainty in other parameters is represented as stated above in Parameter Estimates.

RECOVERY TARGETS

As in previous modelling, we used demographic sustainability as a criterion to set recovery targets for Black Redhorse. Demographic sustainability is related to the concept of a minimum viable population (MVP) (Shaffer 1981). Velez-Espino and Koops (2008) used an allometry, developed by Reed et. al (2003), relating MVP to maximum growth rate. This formula defined MVP as the number of adults required for a 99% probability of persistence over 40 generations (approximately 180 years, given the generation time of 4.5 y ears used in the previous model). We defined MVP as the minimum adult population size that results in a desired probability of persistence over 100 years (approximately 12 generations, given a generation time of 8.2 years), and compared this with results for a 180 year timeframe 22 generations).

Since population growth is not sustainable over time, we simulated the probability of persistence of a stable population over the long-term. To achieve stability in the model, YOY survival was reduced to achieve a geometric mean growth rate (in stochastic simulations) of λ=1.

We estimated recovery targets as follows. (i) 50,000 projection matrices were generated by randomly drawing vital rates based on the means, variances, and distributions as in the population sensitivity analysis, and based on a geometric mean growth rate of λ=1; (ii) projection matrices were drawn at random from these to generate 5,000 realizations of population size per time step (i.e., over 100 years); (iii) These realizations were used to generate a cumulative distribution function of extinction probability, where a population was said to be extinct if it was reduced to one adult (female) individual; (iv) this process was repeated 10 times, giving an average extinction probability per time step. Catastrophic decline in population size, defined as a 50% reduction in abundance, was incorporated into these simulations, and occurred at a probability (P_k) of 0.10, or 0.15 per generation. We used these simulations to determine the number of adults necessary for the desired probability of persistence (see Results) over 100 years. Adults refer to mature (age 4+) individuals.

Minimum area for population viability

Following Vélez-Espino et al. (2010), we estimate the MAPV as a first order quantification of the amount of habitat required to support a viable population. We calculate MAPV for each age-class in the population as

(9) $MAPV_j = MVP_j \cdot API_j$.

MVP_j is the minimum number of individuals per age-class required to achieve the desired probability of persistence over 100 years, as estimated for the recovery target. Individuals were distributed among age classes according to the stable age distribution, which is represented by the dominant right eigenvector (w) of the mean projection matrix based on the growth rate $\lambda = 1$ ($\mathbf{M}\, w = \lambda \cdot w$) (De Kroon *et al.* 1986). API_j is the area required per individual in class j. API was estimated using an allometry for river environments from Randall et al. (1995). This allometry approximates API_j for freshwater fishes based on the total length in mm of class j:

(10) $API = e^{-13.28} \cdot TL^{2.904}$

Space requirements for an age class can increase or decrease throughout the year, depending on the age specific mortality and individual growth for that class. The required space for any given cohort can be described as a function of age (t) by combining equations (4), (6), (9), (10), and the von Bertalanffy growth function as follows:

(11) $$MAPV_t = N_0 \left(\frac{L_\infty e^{-kt}}{L_t} \right)^{-\beta} e^{-13.28} L_t^{2.904}.$$

Taking the derivative of this function with respect to age shows that the space requirements of a cohort can increase or decrease over time, with the maximum space requirements occurring at age t^*; required space increases before this threshold, and decreases after:

(12) $$t^* = t_0 - \frac{1}{k} \ln\left(\frac{-\beta}{2.904} \right).$$

To ensure sufficient space for growth of an age class throughout the year, TL_j and MVP_j for equation (10) were chosen with this in mind; TL and MVP reflected the start of the age class for classes above the threshold, but the end of the age class for classes below the threshold. The latter was achieved by multiplying MVP_j by age specific survival and by API_{j+1}. MAPVs for each age class were estimated separately, and summed to determine stage-specific requirements.

RESULTS

POPULATION SENSITIVITY

Black Redhorse was most sensitive to changes in survival of immature individuals, with elasticities declining to nearly zero as age increased. Likewise, it was more sensitive to perturbations in fecundity of early adults than of late adults. This pattern was more dramatic for a growing population than for a stable one; a stable population was less sensitive to changes in juvenile vital rates and more sensitive to changes in adult vital rates than a growing population, and this difference was significant (Figure 3). Elasticities for a declining population were nearly identical to that of the stable population and are not shown. When considered cumulatively by stage, a growing population was most sensitive to total juvenile survival, and half as sensitive to first year survival, cumulative survival of early adults, or total fecundity of early adults (Figure 4; Table 2). A stable (or declining) population, however, was most sensitive to cumulative survival

of early adults, slightly less sensitive to total juvenile survival, and less than 1/3 as sensitive to YOY survival, cumulative late adult survival, or total fecundity.

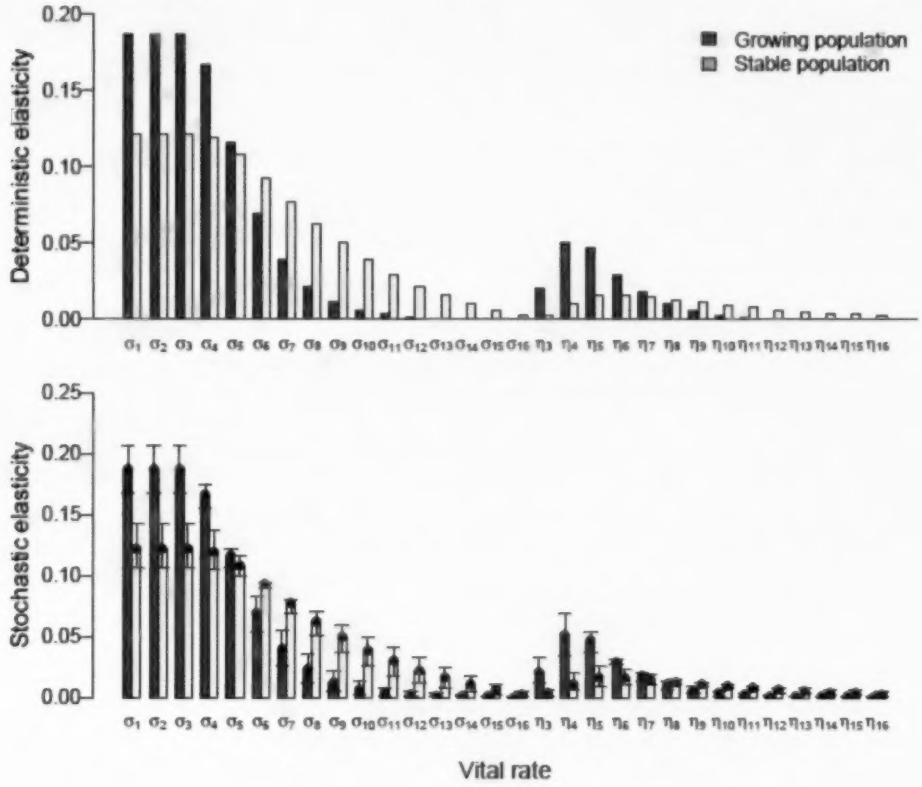


Figure 3. Results of the deterministic (upper panel) and stochastic (lower panel) perturbation analysis showing elasticities (ε_v) of vital rates for Black Redhorse: annual survival probability from age j-1 to age j (σ_j) and fertility at age j (η_j). Results are compared for a growing ($\lambda = 1.6$) or a stable ($\lambda = 1$) population. Stochastic results include associated bootstrapped 95% confidence interval.

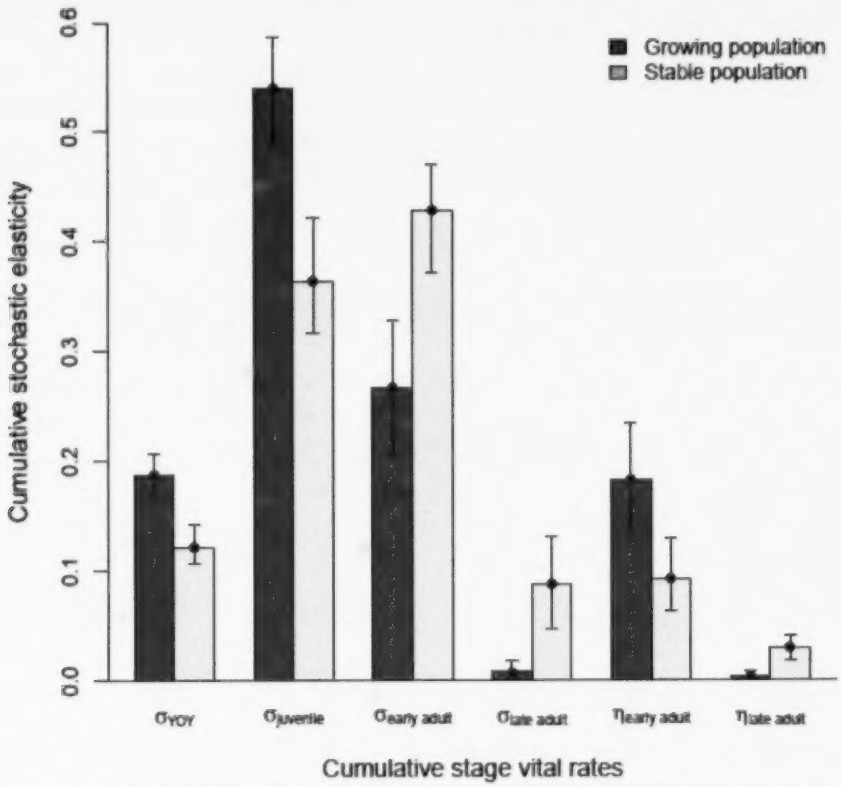


Figure 4. Cumulative stochastic elasticities and bootstrapped 95% confidence bounds for Black Redhorse survival and fecundity by stage for growing and stable populations: first year survival (σ_{YOY}), cumulative survival for juveniles (ages 1-4), and cumulative survival and fecundity for early adults (up to age 10) and late adults (age 11 and over). Exact values in Table 2.

Table 2. Summary of elasticities (deterministic mean, stochastic mean, and bootstrapped 95% confidence bounds) for Black Redhorse vital rates (ε_v) for growing ($\lambda = 1.6$) or stable ($\lambda = 1$) populations. Shown are elasticities for: first year survival (YOY), cumulative survival for juveniles (ages 1-4), and cumulative survival and fecundity for early adults (up to age 10) and late adults (age 11 and over).

Population Status	Elasticity type	Survival				Fecundity	
		YOY (σ_1)	Juvenile ($\sigma_2 - \sigma_4$)	Early adult ($\sigma_5 - \sigma_{10}$)	Late adult ($\sigma_{11} - \sigma_{16}$)	Early adult ($\eta_3 - \eta_{10}$)	Late adult ($\eta_{11} - \eta_{16}$)
Growing	Deterministic	0.19	0.54	0.26	0.01	0.18	0.00
	Stochastic	0.19	0.54	0.26	0.01	0.18	0.00
	Upper bound	0.21	0.59	0.33	0.02	0.24	0.01
	Lower bound	0.17	0.49	0.20	0.00	0.13	0.00
Stable	Deterministic	0.12	0.36	0.43	0.09	0.09	0.03
	Stochastic	0.12	0.36	0.43	0.09	0.09	0.03
	Upper bound	0.14	0.42	0.47	0.13	0.13	0.04
	Lower bound	0.11	0.32	0.37	0.05	0.06	0.02

RECOVERY TARGETS

Probability of extinction decreases as a power function of population size (Figure 5). Functions of the form $y = a \cdot x^{-b}$ were fitted, using least squares and the logged values of x (population size) and y (extinction probability), to the simulated extinction probabilities for each catastrophe scenario.

While choosing a larger recovery target will result in a lower risk of extinction, there are also costs associated with an increased target (increased recovery effort, longer time to recovery, etc.). When determining MVP from the fitted power curves, we attempted to balance the benefit of reduced extinction risk and the cost of increased recovery effort with the following algorithm. (i) We assumed that the maximum allowable risk of extinction is 10% based on COSEWIC's quantitative criteria (E) that a risk of extinction greater than or equal to 10% within 100 years constitutes Threatened status. We define a maximum MVP (i.e., maximum feasible effort) to be the population that would result in a 0.1% probability of extinction, as this is the most stringent criteria in the literature; (ii) using these as boundaries, we calculate the average decrease in probability of extinction per individual increase in population size; (iii) we choose as MVP the population size that would result in this average (i.e., the point on the power curve at which the slope equals the average % decrease in extinction risk per increase in target). This represents the point between the upper and lower boundaries where the reduction in extinction risk per investment in recovery is maximized.

Calculated in this way, MVP was approximately 130 adults (ages 4+) when the probability of catastrophic decline (50% decline) was assumed to be 10% per generation (1.3% annually). If catastrophes occurred at 15% per generation (2.0% annually), MVP was approximately 270 adults (see Table 3 for MVP of juveniles and YOY). In both scenarios, the cumulative probability of extinction for the respective MVPs was approximately 1.5% over 100 years (Figure 5). The extinction risk, P(ext.), for the 10% (Equation (11)) or 15% (Equation (12)) per generation catastrophe scenario can be defined as a function of initial adult population, N, as:

(13) $$P(ext.) = 3067 \cdot N^{-2.506}$$

(14) $$P(ext.) = 962 \cdot N^{-1.985}.$$

If catastrophes occur at 15% per generation and the recovery target is set based on an assumption that catastrophes occur at 10% per generation, the risk of extinction will be greater than 5%.

MVP simulations assumed an extinction threshold of 1 adult female (or 2 adults). We observed that assuming a higher, quasi-extinction threshold (i.e., if the population is considered effectively extinct before it declines to 1 female) results in a roughly linear increase in MVP. For example, if the quasi-extinction threshold is defined as 50 adults, and the chance of catastrophe is 15% per generation, mean MVP increases from 270 adults to ~1700 (range ~1400 – 2100) (Table 3). Thus, if the true extinction threshold is greater than 1 adult female, larger recovery targets should be considered. Equations describing extinction risk at a threshold of 50 adults, and a probability of catastrophe of 10% and 15%, respectively, are as follows:

(15) $$P(ext.) = 110177 \cdot N^{-2.376}$$

(16) $$P(ext.) = 140762 \cdot N^{-2.157}$$

MVPs were also calculated for a 15% probability of catastrophe and a 180 year timeframe for comparison with results from previous modelling (Vélez-Espino and Koops 2008). MVP for extinction thresholds of 1 (equation (15)) or 50 adults (equation (16)) were 930 or 5810 adults

(range ~5000 – 7100), respectively. Targets from Vélez-Espino and Koops (2008) ranged from ~7600 – 8000.

(17) $$P(ext.) = 607 \cdot N^{-1.572}$$

(18) $$P(ext.) = 13669 \cdot N^{-1.599}$$

Minimum area for population viability

The stable stage distribution of Black Redhorse is 99.89% YOY, 0.08% juvenile (ages 1-3), and 0.03% adult (ages 4-16) (Table 4). Note that this distribution assumes a post-breeding census such that the YOY class consists of individuals that are freshly hatched and have not experienced any mortality, and therefore constitute the majority of the age distribution. MAPV ranged from 1.1 ha for an MVP of 130 adults to 14.5 ha for a target of ~1700 adults (for a timeframe of 100 years) or 49.1 ha for a target of 5800 adults (for a timeframe of 180 years) (Table 3). We recommend the MAPV that corresponds to a probability of catastrophe of 15%, an extinction threshold of 50 adults, and an extinction risk of ~0.015, or 14.5 ha (range 12.2 – 17.8) for 1700 adults, 3900 juveniles, and 5 million YOY. These areas assume that each individual requires the areas (API) listed in Table 4, and does not account for any overlapping of individual habitats (sharing) that may occur. It is important to note that this area is based on an allometry of fish density per fish size and does not include any additional space requirements for the completion of life stages (for example, requirements for migration from resident habitat to spawning habitat).

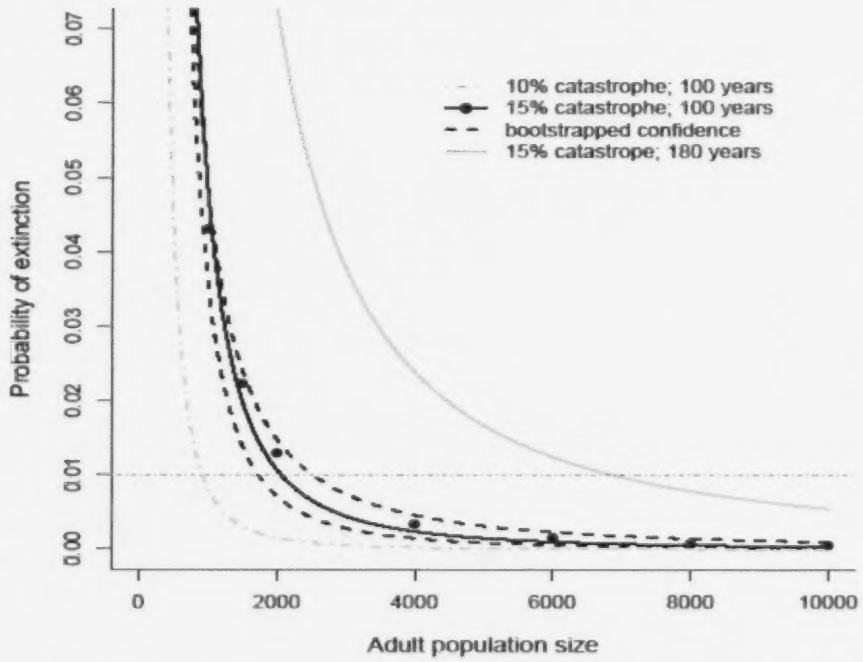


Figure 5. Probability of extinction within 100 years of 10 simulated Black Redhorse populations, at equilibrium, as a function of adult population size. Curves represent different combinations of the probability of catastrophe per generation (%), and timeframes (11 or 180 years. All curves represent extinction thresholds of 50 adults. Dashed horizontal reference line is at 0.01 and intersects curves at the associated MVPs (Table 3).

Table 3. Number of individuals by stage required to support a minimum viable population (MVP), and associated hectares of habitat required, based on estimated Area per Individual (Table 4). Results for two different extinction thresholds, two probabilities of catastrophe, and two different timeframes are shown. Stages shown are young of the year (YOY), Juvenile (ages 1-3), adult (ages 4-16).

Extinction Threshold	Generational Catastrophe	Time-frame	Reference Equation	Age Class	MVP	MAPV (ha)
2 adults	10%	100 years		YOY	3.8 x10^5	0.04
				Juv	230	0.28
				Adult	130	0.78
				Total		1.10
2 adults	15%	100 years		YOY	7.8 x10^5	0.07
				Juv	612	0.58
				Adult	270	1.62
				Total		2.27
50 adults	10%	100 years		YOY	2.2 x10^6 (2.0x10^6 - 2.6*10^6)	0.21 (0.19 - 0.25)
				Juv	1760 (1590 - 2060)	1.67 (1.51 - 2.00)
				Adult	770 (690 - 900)	4.60 (4.15 - 5.40)
				Total		6.49 (5.85 - 7.61)
2 adults	15%	180 years		YOY	2.7 x10^6	**0.3**
				Juv	2,130	**2.0**
				Adult	930	**5.6**
				Total		**7.9**
50 adults	**15%**	**100 years**		**YOY**	**5.0x10^6 (4.2x100^6 - 6.1x10^6)**	0.5 (0.4 - 0.6)
				Juv	**3920 (3291 - 4820)**	3.7 (3.1 - 4.6)
				Adult	**1720 (1440 - 2110)**	10.3 (8.6 - 12.7)
				Total		14.5 (12.2 - 17.8)
50 adults	15%	180 years		**YOY**	1.7x10^7 (1.5x10^7 - 2.1x10^7)	1.6 (1.4 - 1.9)
				Juv	13280 (11500 - 16130)	12.6 (10.9 - 15.3)
				Adult	5810 (5040 - 7060)	34.9 (30.2 - 42.3)
				Total		49.1 (42.5 - 59.6)

Table 4. Stable stage distribution (SSD; percentage of the population in each stage, assuming a pre-breeding census. i.e., the YOY class is nearly 1 year old, age 1 class is nearly 2 years old, etc.) and required area per individual (API) for each age class.

Age class	SSD (%)	API (m^2)
YOY	99.89	0.04
Juvenile	0.08	4.1 – 25.6
Adult	0.03	38.7 – 107.0

DISCUSSION

Our results show that to avoid jeopardizing the survival and future recovery of Black Redhorse in Canada, human-induced harm to the annual survival of juveniles and early adults should be minimal. Changes to survival of YOY and fecundity of early adults had much less influence on population growth. Changes to survival and fecundity of older adults had minimal impact.

Recovery targets, based on the concept of MVP, were presented for a variety of risk scenarios. Recommended MVP targets for Black Redhorse are 1700 adults (ages 4+) and 3900 juveniles (ages 1-3), assuming the probability of a catastrophic (50%) decline is 0.15 per generation and an extinction threshold of 50 adults. According to Reed *et al.* (2003), catastrophic events (a one-time decline in abundance of 50% or more) occur at a probability of 0.14 per generation in vertebrates. Recommended MAPV for Black Redhorse was 14.5 ha of good quality, suitable habitat, including 3.7 ha for juveniles, and 10.3 ha for adults (if these habitats are discrete).

We emphasize that the choice of recovery targets is not limited to the recommended target, or to the scenarios presented inTable 3. Required adult population sizes can be calculated for any alternative probability of extinction using one of equations (11) to (16) depending on which risk scenario (probability of catastrophe and extinction threshold) best represents the Canadian population of Black Redhorse, and what level of risk is considered acceptable.

We also emphasize that recovery targets based on MVP can be easily misinterpreted (Beissinger and McCullough 2002) as a reference point for exploitation. A recovery target pertains exclusively to a minimum abundance level for which the probability of long-term persistence within a recovery framework is high. Therefore, abundance-based recovery targets are particularly applicable to populations that are below this threshold, and are useful for optimizing efforts and resources by selecting those populations that are in the greatest need of recovery. We stress that these MVP targets refer to adult numbers only. If juveniles are being included in abundance estimates, then the MVP should include these age classes as well (see Table 3).

PREVIOUS MODELLING

This modelling exercise differed from previous modelling of Black Redhorse (Vélez-Espino and Koops 2008; Vélez-Espino and Koops 2009a) in a number of ways. Maximum age of Black Redhorse in Ontario was found to be much older (16 years) than the maximum age of the species in Missouri (11 years) that was used for previous modelling. Annual survival as estimated from Ontario sampling also differed from that used in previous modelling. Finally, previous modelling relied on a relationship between MVP and maximum population growth rate to estimate MVP, while this model used stochastic simulations and incorporated estimated parameters and uncertainty for the specific population under consideration.

Elasticities, when considered cumulatively by life stage, were very similar to those determined by previous modelling except for juvenile survival; juvenile survival was similar to the elasticity for YOY survival in previous modelling, but was more similar to the elasticity for adult survival in this model. In addition, we compared elasticities for a growing and a stable population, while previous modelling considered only a stable population.

The recovery targets determined by previous modelling were higher than those recommended by this model. The discrepancy was primarily due the methodology used (simulation versus allometry). Simulated extinction risk is strongly influenced by how parameter variance is defined; more accurate estimates of parameters and environmental variation will improve the reliability of recovery target estimates. Differences in life history, such as those introduced by incorporating parameters specific to the Canadian population, can also contribute to differences in recovery targets (e.g. Young and Koops 2012)

UNCERTAINTIES

Our estimates of required habitat (MAPV) assume that habitat is of high quality throughout the range of Black Redhorse. We did not have sufficient data to either confirm, or provide an alternative to this assumption.

MVP targets differed dramatically based on the assumed frequency of catastrophic decline (c.f. Vélez-Espino and Koops 2012). If recovery targets are set based on an incorrect rate of catastrophes, risk of extirpation will be greater. Further research in this area is warranted.

Black Redhorse age data from the Missouri Ozarks suggest that maximum age and size, and growth rates may vary among creeks and rivers in the same region (Beckman and Howlett 2013). Data from the Grand River exclusively were used for this model and may not reflect the characteristics of other SW Ontario populations.

Finally, predictions from this model assume random mating and complete mixing of the population (i.e., all individuals interact and can reproduce with one another). This assumption should be considered when applying MVP targets, and larger total targets should be set if the assumption does not hold.

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